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2018-01

Kauppi , L , Norkko , A & Norkko , J 2018 , ' Seasonal population dynamics of the invasive polychaete genus *Marenzelleria* spp. in contrasting soft-sediment habitats ' , Journal of Sea Research , vol. 131 , pp. 46-60 . <https://doi.org/10.1016/j.seares.2017.10.005>

<http://hdl.handle.net/10138/308896>

<https://doi.org/10.1016/j.seares.2017.10.005>

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Full citation: Kauppi L, Norkko A, Norkko J (2018) Seasonal population dynamics of the invasive polychaete genus *Marenzelleria* spp. in contrasting soft-sediment habitats. *Journal of Sea Research* 131:46-60.

Seasonal population dynamics of the invasive polychaete genus *Marenzelleria* spp. in contrasting soft-sediment habitats

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Abstract

Three species of the invasive polychaete genus *Marenzelleria* are among the dominant benthic taxa in many, especially deeper, areas in the Baltic Sea. The population dynamics of the polychaetes in the Baltic are, however, still largely unknown. We conducted monthly samplings of the benthic communities and environmental parameters at five sites with differing depths and sediment characteristics in the northern Baltic Sea (59°50.896', 23°15.092') to study the population dynamics, productivity and growth of *Marenzelleria* spp. from April 2013 to June 2014. The species of *Marenzelleria* occurring at the study sites were identified by genetic analyses. At the deepest site (33 m) only *M. arctia* was present, while all three species were found at the shallower, muddy sites (up to 20 m depth). At the shallow (6 m) sandy site only *M. viridis* and *M. neglecta* occurred. The sites differed in the seasonal dynamics of the *Marenzelleria* spp. population, reflecting the different species identities. The muddy sites up to 20 m depth showed clear seasonal dynamics, with the population practically disappearing by winter, whereas more stable populations occurred at the deepest site and at the sandy site. The highest density, biomass and production were observed at the 20 m deep, organic-rich muddy site where all three species recruited. The seasonally very high densities are likely to have important consequences for organic matter processing, and species interactions at these sites. The observed high productivity of the populations has possibly facilitated their establishment, and considerably increased secondary production in especially the deeper areas.

Key words: invasion, spionid polychaete, productivity, *Marenzelleria viridis*, *Marenzelleria neglecta*, *Marenzelleria arctia*

1 Introduction

Communities are composed of populations of individuals of different species, and their interactions lie at the heart of ecological research. To understand single observations, we need to consider them in the context of the interacting individuals or populations for them to have any relevance. Change both in space and time is an intrinsic attribute of natural ecosystems, and a dynamic population is expressing these changes responding to changes in both the abiotic and biotic environment. Studying the populations and their dynamics will thus give us an insight into their possible interactions with their environment and is therefore essential from a conservation and management point of view (Ranasinghe et al., 2012).

Invasive species are often seen as a threat to native ecosystems due to their possible negative effects on biodiversity and ecosystem functioning (Ehrenfeld, 2010; Mack et al., 2000). Due to their demonstrated and hypothesized negative effects, a large part of research in invasion ecology focuses on how to prevent invasions or how to manage already established populations. In trying to manage invasiveness and predict the spread of populations, as well as their interactions with the environment, knowing the species' population biology is essential. On the other hand invasions also offer a great opportunity to study basic processes in population dynamics (Sakai et al. 2001). How the system will respond to an invasion depends on the properties or traits of the introduced species as well as the properties of the system being invaded, and their interaction (e.g. Bohlen et al. 2004). Therefore it becomes increasingly important to know both your species, and your system when analyzing the effects of the invasion on for example ecosystem functioning. Studying population dynamics and factors affecting it also enables us to make predictions about the future population under changing environmental conditions.

The polychaete genus *Marenzelleria* spp. was first observed in the Southern Baltic Sea in 1985 and by 1990 it had reached the northern Baltic Sea (Bick and Burkhardt 1989, Stigzelius et al. 1997, Norkko et al. 1993). Now the genus occurs nearly everywhere in the Baltic with a total of three species of the genus observed (Kauppi et al. 2015, Bastrop and Blank 2006, Blank et al. 2008). *M. viridis* (Verrill, 1873) and *M. neglecta* Sikorski and Bick, 2004 are of North American origin, and *M. arctica* (Chamberlin, 1920) of European arctic origin (Blank et al. 2008). *M. viridis* has also been introduced to the Pacific coast of North America (e.g. Ranasinghe et al. 2012). The population and recruitment dynamics of the different species over the year are largely unknown in the Baltic Sea. Previous results on population dynamics and settling of larvae (e.g. Simm et al. 2003) have to be questioned due to the uncertainty in species identification, which is only possible by genetic analyses (e.g. Blank et al. 2008). Given that the invasive polychaete genus is one of the most dominant benthic species in many areas around the Baltic Sea (Kauppi et al. 2015), it is surprising how little we know about its basic biology and ecology. Even the occurrence and habitat preferences of the three different species are unknown in most of the Baltic Sea. Furthermore, its effects on the ecosystem functioning, for example affecting nutrient cycling through bioturbation and bioirrigation, might be substantial and vary over seasons and areas, and between the three species (Kauppi et al. 2017, Renz and Forster 2013 and 2014, Norkko and Reed et al. 2012, Hietanen et al. 2007). Additionally, few studies have during recent decades quantified seasonal changes in the macrofauna communities or their productivity in the Baltic Sea over a whole year leaving a large gap in our knowledge about the dynamics of this system over the winter, and after changes in species composition have taken place (but for some older studies see e.g. Segerstråle 1937, 1962, Sarvala 1971, Elmgren 1978, Elmgren et al. 1986, Uitto and Sarvala 1991, Lehtonen 1996).

Our aim was to study seasonal dynamics and factors affecting the populations of *Marenzelleria* spp. in the northern Baltic Sea, and analyze the growth and productivity of *Marenzelleria* spp. populations from shallow (5 m) to deep (33 m) coastal habitats. A further aim was to identify the

species present at the study sites, for which genetic material was collected. This was done in order to better understand and predict the future impacts of this species complex on the Baltic Sea ecosystem.

2 Material and methods

2.1 Sampling design

Population dynamics of *Marenzelleria* spp. were studied at five different locations in the proximity of Tvärminne Zoological Station in the southernmost Finland (59°50.896', 23°15.092'). Site I is a muddy, unvegetated site with a depth of 5-6 m situated at the inlet into a bay. Site II is an unvegetated, muddy site at 10 m depth. Site III has a depth of 20 m and the sediment consists of a looser muddy layer on top of more dense clay. Site IV has a depth of 33 m and very loose mud bottom. Site V also has a depth of 5-6 m but in contrast to site I, this site is more exposed to winds and wave action from the open sea, and has sandy sediment.

At sites I-IV sampling was conducted monthly starting in April 2013 and ending in June 2014, with the exception of December 2013 and February and April 2014, when sampling was not conducted due to challenging winter conditions. Site V was sampled from May 2013 onwards monthly until December 2013, except in November, and again in March and June 2014. In April and May 2013 at sites I-IV, three replicate samples were taken with a Limnos sediment corer (9.3 cm in diameter) from the ice or from a small boat. From June 2013 until June 2014, three replicate samples were taken with a Gemax twin corer (9 cm in diameter) at sites I and III and five replicate samples at sites II and IV. At site V six replicate samples were taken by SCUBA diving using acrylic core liners with a diameter of 5.6 cm.

The top 1 cm of the core samples was sliced and sieved gently through a 200- μ m sieve in order to collect the newly settled larvae. The total depth of the sediment in the cores varied from 8 cm at site V (sandy sediment) to approximately 30 cm at sites I to IV, always extending below the depth of the fauna in the sediment at the site. The rest of the sample was sieved through a 500- μ m sieve. The benthic samples were fixed in 70 % ethanol and dyed with rose Bengal and sorted later under microscope. Biomasses are reported as g wet weight m⁻² of blotted individuals, which means that the biomass of newly settled specimens is not included due to their small size.

2.2 Environmental factors affecting densities and biomasses at the different sites

In addition to benthic core samples, a number of environmental parameters were measured on each sampling occasion. Data from the near-bottom water (<1 m) for temperature and salinity were obtained with a CTD device and oxygen (mg L⁻¹ and %) was measured with an YSI proODO oxygen meter. Sediment organic content (measured as loss on ignition, LOI), C/N ratio and grain size were determined from the top cm of sediment from an additional core taken at each site at each time. For determination of the organic content, the sediment was first dried at 60°C for 48 hrs and thereafter burned at 500°C for 3 hrs and the organic content was calculated from the difference in weight of the samples. For C/N, approximately 30 mg (sandy sediment) or 10 mg (muddy sediment) of dried (60°C for 48 hrs), acidified sediment was analyzed for carbon and nitrogen content. Grain size distribution was determined by sieving the sediment sample through a series of sieves (2, 1, 0.5, 0.25, 0.125 and 0.063 mm) after which the sediment retained in the sieves or in the pan was dried (60°C for 48 hrs) and weighed.

Pearson product moment correlations were calculated between environmental factors (temperature, salinity and dissolved oxygen (DO) in the bottom water, sediment organic content (OM) and C/N) and the average density of *Marenzelleria* spp. per sampling (an average of 3 to 6 replicates per sampling, depending on the site) to investigate relationships between the seasonal variation in the environment and the density of the *Marenzelleria* spp. population. Due to autocorrelation in the

time series, correlations were also calculated between the density at t+1 and the environmental predictors at time t.

2.3 Population dynamics, growth and production

The maximum width of *Marenzelleria* spp. at the widest part of the worm (usually near the 10th segment) was measured with an ocular micrometer and used as an estimate of size to identify cohorts and to measure growth. Biomass of all species was measured as wet weight of blotted animals. For growth measurements of *Marenzelleria* spp., selected individuals from representative size classes were remeasured and dried for 48 h at 60°C and weighed. The dry weight was regressed against the width of the worm and the regression was then used to convert the width of all specimens to biomass.

Different cohorts were identified to estimate recruitment, longevity and growth of the individual in the population following the method of Bhattacharya (1967) (TropFishR -package¹). Secondary production and production to biomass -ratios (P/B -ratio) for each cohort were calculated following Brey (2001). The Increment Summation Method (ISM) was used to assess the production and P/B -ratios for the whole population (Brey 2001).

2.3.1 Individual growth rates and factors affecting growth

Individual growth rates were modeled using the von Bertalanffy growth equation (Brey, 2001). Both the specialized and generalized von Bertalanffy growth models were tested. Generalized von Bertalanffy growth model had the best fit for all cases:

$$S_t = S_{\infty} * (1 - e^{-K*(t-t_0)})^D$$

where S_t is size at time t, S_{∞} is the infinite size of the species, K is the growth constant defining how fast the asymptote is reached, and D is the shape parameter determining the shape of the curve, which is more or less sigmoid.

The growth parameters were defined separately for all the sites. At site IV with the confirmed occurrence of only one species, and at site V with the confirmed occurrence of two species, the growth parameters were also iterated separately for the distinguishable cohorts during the initial phase of their growth before the growth reached a plateau. At site IV there were two separable cohorts that could be followed from their settling throughout the study period: cohort C2 settled in May 2013 and cohort C3 settled in early July 2013. At site V, four cohorts could be separated: C2 settled in May 2013, C3 settled in June 2013, cohort C4 settled in early July 2013 and cohort C5 settled in October 2013.

To investigate possible intra- and interspecific relationships affecting growth, individual growth in mg d^{-1} for every cohort during each sampling interval from t to t+1 were correlated with the density of *Marenzelleria* spp. in the cohort at time t, with the total density of *Marenzelleria* spp., the total density of other macrofauna, and the growth rates of other cohorts.

2.4 Species identities of *Marenzelleria* spp.

An accurate identification of the three species of *Marenzelleria* spp. occurring in the Baltic Sea, *M. viridis*, *M. neglecta* and *M. arctica*, is only possible with genetic analyses. A selection of worms from all sites were stored in ETAX-A and sent to the University of Rostock, Germany, for genetic analyses.

For an analysis of the proportions of the different species in the whole population about 200 worms would need to be analyzed, which was not possible and not intended in this study. The number of worms analyzed per site was 13 (I), 8 (II), 8 (III), 18 (IV) and 4 (V). All worms analyzed from the

sandy site V belonged to either *M. viridis* or *M. neglecta*. At the muddy sites I to III all three species were observed, whereas at the deepest site IV the only species observed was *M. arctia*. Because the 200 worms needed for a reliable analysis of the proportions of the different species in the populations were not obtained, we will refrain from using the species names and refer to the worms as *Marenzelleria* spp. at all sites, discussing the potential differences in the dynamics with reference to the sites with only one (site IV) or two species (V) observed throughout the study period.

3 Results

3.1 Hydrography and sediment properties

The lowest temperatures in the near bottom water at the muddy sites I–IV were recorded in April 2013 (0.04–0.6°C, depending on the site) when ice still covered the shallowest sites I and II (table 1). The winter 2012–2013 was extremely cold and ice cover that formed around Tvärminne Zoological Station in November lasted until late April 2013. The winter 2013–2014 on the other hand was very mild, with ice cover only for a short period in February in the inner bays. At the sandy site V, the lowest temperature was recorded in March 2014 (2.2°C). The highest temperatures at the shallowest sites I and V were recorded in late July 2013, and at sites II and III in August 2013, whereas the highest temperature at the deepest site IV was recorded in June 2013. The highest temperatures ranged from 9.1°C at site IV to 16.1°C at site I.

Salinities over the year ranged from 4.6 at site I in early July to 7.1 at site IV in October (table 1). At all sites there was a period of higher than average salinity from Sept/Oct 2013 to December/January 2014 (depending on site). Also in May 2013 (sites I–IV) and later in July (all sites) higher than average salinities were recorded.

None of the sites went anoxic at any point during the year. The lowest oxygen concentration was measured at the deepest site IV in August (4.98 mg L⁻¹), and the highest at site II (20 m) in May 2013 (table 1). In general the highest oxygen concentrations at all muddy sites were recorded in May 2013, and higher than average oxygen concentrations at all sites occurred under the period from Nov 2013 until May 2014.

The seasonal dynamics of the organic content in the sediment varied between the sites (table 1). The sandy site V had the lowest organic content of all sites (0.7–1.1 %). The lowest organic content (0.7%) was measured in Oct 2013. At the shallow muddy site I the organic content varied from 2.6%, which was the lowest organic content measured at all the muddy sites, to 11.2%. At site II the organic content ranged from 5.3 to 12.5% and at site III fairly similarly from 4.1 to 13.5%. At the deepest site IV (33 m), the organic content was high and relatively stable over the whole study period (12.8–15.3%) with a slight decrease from early July to September and November to January.

Sediment grain size at site I varied from very fine sand to coarse silt, at site II from very coarse to coarse silt, at site III from very coarse to coarse silt, and at site V from fine to very fine sand. At site IV the grain size was defined as coarse silt on all sampling occasions.

3.2 Densities and biomasses of *Marenzelleria* spp.

The densities and biomasses at sites I and II showed similar dynamics peaking from March to May, but then falling very sharply in summer. Population dynamics at sites III to V differed from both each other and from sites I and II. Site III showed two peaks in both densities and biomasses, in June-August 2013 and in May 2014. Site IV had the most stable densities and biomasses of adult worms over the year (fig. 1) with a slight peak in June-July. Site V had high densities in spring, which decreased towards the winter, whereas biomass varied similarly to other sites. See fig. 1 for monthly average densities and biomasses over the year. In addition to *Marenzelleria* spp., the most common species found at the sampling sites were the clam *Macoma balthica*, the cockle *Cerastoderma edule*, Oligochaeta, snails of the family Hydrobiidae, the polychaetes *Hediste diversicolor*, *Pygospio elegans* and *Manayunkia aestuarina*, and at the deepest site the amphipod *Monoporeia affinis*.

3.2.1 Sites I and II

At sites I and II the densities of newly settled worms peaked in May in 2013 (note that the sampling was started in April), whereas in 2014 the peak densities of juveniles were observed in March and May at site I (on average 14383 ind m⁻²) and in May at site II (on average 15813 ind m⁻²). The newly settled individuals first appeared in the samples in January in 2014. Sporadic newly settled individuals were observed at both sites in July and August. The adult densities at both sites I and II were moderate to even non-existent. Only single adult worms were observed with the highest average density being 472 ind m⁻² at site I, and 314 ind m⁻² at site II, both observed in August.

The highest biomass (in wet weight) of *Marenzelleria* spp. at both site I and II was observed in May 2014 (on average 15.3 and 6.9 g m⁻², respectively). Lowest biomasses at site I, apart from the observation of zero worms in November, were observed in early July 2013 and in June 2014 (on average 0.8 and 0.7 g m⁻², respectively), and at site II in early July 2013 (on average 0.01 g m⁻²).

3.2.2 Sites III, IV and V

At site III newly settled individuals were observed on all sampling occasions except in September and November. Peak densities of juveniles were observed from March to May and from early July to August. Site III had the highest adult densities in the study (max 5135 ind m⁻² in one core). High adult densities were observed from early July to August 2013 and in June 2014. After August the densities however dropped to an average of 419 ind m⁻² for the period September–March. The highest average biomass was observed in August 2013 (13.2 g m⁻²), and high biomasses occurred also in late July 2013 (11.2 g m⁻²) and June 2014 (11.6 g m⁻²). The lowest biomasses were measured in April 2013 and in March 2014 (0.4 g m⁻²), although in May 2013 all worms were under the detection limit of 0.003 g.

At the deepest site IV juveniles were observed in May and from early July to September 2013, and in March 2014. The densities of the juveniles peaked in May and July 2013 and in March 2014. This site had the lowest average density (1554 ind m⁻²) but the most stable population of adult *Marenzelleria* spp. occurring over the entire year. The highest adult densities were observed from June to August 2013 and in June 2014 (max 2200 ind m⁻² per core). The highest biomass (9.2 g m⁻²) was measured in June 2014, and high biomasses were also observed in late July and August 2013 (5.1 and 7.4 g m⁻², respectively). The lowest biomasses were observed in April and May 2013 (0.8 and 0.4 g m⁻², respectively).

At the only sandy site of the study, site V, juveniles were observed in the samples from May to August and in October 2013, and in March and June 2014. The highest juvenile densities were observed in May 2013 and June 2014 (on average 7684 ind m⁻², maximum 11780 ind m⁻² per core). On average this site had the second highest densities overall from all five sites. The highest adult

density was observed in June 2013 (on average 2437 ind m^{-2} , maximum 4062 ind m^{-2} per core observed in late July and September). The highest average biomass was observed in September 2013 (8.3 g m^{-2}) and the lowest in May 2013 (1.1 g m^{-2}). The lowest average biomass was nevertheless quite high compared to the other sites.

3.3 Relationship between environmental factors and densities

Significant correlations are mentioned in the text and in figure 2, for all results see table 2. At site I, *Marenzelleria* spp. density had a significant positive correlation with DO ($R=0.622$, $P=0.041$) and a significant negative correlation with OM ($R=-0.682$, $P=0.014$) (see fig. 2 and table 2 throughout). At site II, the density only correlated significantly with DO ($R=0.688$, $P=0.025$). At site III, the density at time t or $t+1$ did not correlate significantly with any of the environmental factors. At site IV, the density had a significant correlation only with DO ($R=-0.586$, $P=0.045$). At the sandy site V, density correlated significantly with salinity ($R=-0.782$, $P=0.008$) and OM ($R=0.775$, $P=0.024$).

3.4 Life cycle, cohort settlement and growth of *Marenzelleria* spp.

Based on the cohort and size-frequency analyses (fig. 3) we estimate a maximum life span from the settlement until the last observation for the adults of 434 days (=1 year and 2 months) at site III. At the other sites the estimated life span for adults after settlement lies between 373 (site II) and 403 days (site IV). The estimates of t_0 (when the width of the individuals is 0) from the von Bertalanffy equation (table 3) varied from 27 days (=under 1 month) to 125 days (=4 months). Estimated for the individual cohorts at sites IV and V, t_0 varied from 125 to 136 days (=4 to 4.5 months).

The number of cohorts recruited per year varied between sites. At sites I and IV, recruitment of two cohorts per year could be distinguished, whereas at sites II and III we could distinguish three cohorts recruited per year. At the sandy site V we can distinguish four cohorts recruiting in year 2013. At sites I–III and V one cohort seemed to survive from the previous year, in contrast to site IV, which seemed to have two cohorts surviving from year 2012 (fig. 3). The large individuals seemed to be gone from all sites during winter but appeared again in the samples in spring and summer. Juveniles dominated the density but, when present, the large specimens often dominated biomass at all sites.

The highest individual growth parameters (table 3) estimated for all cohorts combined with the general von Bertalanffy growth equation were observed at site IV ($K=0.006$) and the lowest growth parameters were estimated for site V ($K=0.001$). Site I and II had a K of 0.002 and site III a K of 0.003.

At sites IV and V with the presence of only one and two species of *Marenzelleria* spp. confirmed, respectively, the growth parameters were also estimated for the cohorts separately. At site IV, the cohort CI_0 (settled in May 2013) had the highest K (0.007), and the cohort C3 had a K of 0.002. When estimated for the initial phase of growth before reaching the plateau, the cohort C2 had a K of 0.021, whereas for cohort C3 the K during the initial phase was 0.012. At site V, the first, second and third cohorts C2, C3 and C4 settling in May, June, and early July 2013, respectively, had the highest K parameters (0.019, 0.013 and 0.01). The cohort CIV_0 settling in October 2013 had the lowest K of 0.004.

Mean individual growth rates as mg dwt $ind^{-1} d^{-1}$ were calculated between each sampling occasion (table 4). At site I the mean individual growth rate (as mg dwt $ind^{-1} d^{-1}$) decreased for both cohorts settling in 2013 from early July to August (from 0.06 in early July to 0.02 in August for cohort C2 and from 0.01 to -0.01 for cohort C3). After the winter in March the growth rates for both cohorts was 0.02, and for the cohort C4 settling in March 2014, the growth rate increased from 0.01 after settling to 0.02 in May. At site II the cohorts C2 and C3 settling in March and early July, respectively, the growth rates increased during summer from May (0.002) to September (0.04) for

C2, and from 0.01 from the settling in early July to 0.08 in August for C3. The growth rates decreased again for winter for all cohorts settling in 2013 reaching a low of -0.02 in January for cohort C3. For the cohort C4 surviving after winter, the growth rate again increased to 0.04 in May 2014. At site III, the cohort settling in April had the highest growth rate in May 2014 (0.1) and the lowest in August (-0.002), the cohort settling in June had the highest growth rate in October (0.02), and the lowest in January (0.005), and the cohort settling in October had the highest growth rate in June 2014 (0.004) and the lowest in October (0.0005). For site IV, both cohorts settling in 2013 had the lowest growth rates in August (0.0003 and -0.005 for C2 and C3, respectively). The May-cohort C2 had the highest growth rate in early July (0.03), whereas the early July-cohort C3 had the highest growth rate in March/May 2014 (0.02). For the sandy site V cohorts the lowest growth rates varied from 0.0007 in October (C4) to 0.008 in March (C2), and the highest from 0.009 in October (C5) to 0.03 in May and June 2013 (C2 and C3).

3.5 Possible intra- and interspecific relationships

The results from the correlation tests done to investigate possible intra- and interspecific relationships affecting growth (significant results are mentioned in the text, for all results, see table 5) showed correlations between the growth rates and densities of *Marenzelleria* spp. and other species at site I, but there were no statistically significant correlations at the $\alpha=0.05$ level. In general the number of taxa correlated negatively with the growth rate of the first cohorts, and density of other taxa correlated negatively with the growth rates of the second and third cohorts. The growth rate of the second cohort also correlated negatively with the density of *Marenzelleria* spp. in the first cohort. Otherwise the correlations were positive. At site II there were no significant correlations, but the density of *Marenzelleria* spp. in the second cohort and the total density of *Marenzelleria* spp. correlated negatively with the growth rate of the first cohort ($R=-0.626$ and $R=-0.6333$, respectively). At site III, the density of *Marenzelleria* spp. in the third cohort had significant negative correlation with the growth rate of the first cohort ($R=0.97$, $P=0.00007$). Number of taxa also correlated negatively with the growth of the second ($R=-0.599$, $P=0.067$) and third cohort ($R=-0.974$, $P=0.026$), and the total density of *Marenzelleria* spp. correlated negatively with the growth of the second cohort ($R=-0.657$, $P=0.039$). At site IV, the density of *Marenzelleria* spp. in the first cohort had a significant positive correlation with the growth in that cohort ($R=0.865$, $P=0.001$), otherwise the correlations were low and not significant. At site V, the density of *Marenzelleria* spp. in the first cohort correlated positively with the growth in that cohort ($R=0.806$, $P=0.053$) and in the second cohort ($R=0.750$, $P=0.086$). The *Marenzelleria* spp. density in the second cohort and the total *Marenzelleria* spp. density also correlated positively with the growth in the second cohort ($R=0.894$, $P=0.016$, and $R=0.927$, $P=0.008$ for density in the second cohort and in total, respectively). The density in the second cohort also had a significant positive correlation with the growth in the third cohort ($R=0.940$, $P=0.002$). The number of taxa, on the other hand, had a negative correlation with growth of the third cohort ($R=-0.683$, $P=0.091$), and the density of the fourth cohort also had a negative correlation with the growth of that cohort ($R=-0.999$, $P=0.031$).

3.6 Production and growth

Secondary production by growth (in mg dw) was calculated for each cohort separately and assessed for the whole population of *Marenzelleria* spp. by using the increment summation method (Table 6). Also elimination is presented in table 6 but not further discussed. The highest total secondary production (as dry weight) over the study period from April 2013 to June 2014 occurred at the muddy site III (182.4 mg m^{-2}), and the lowest at the deepest site IV (10.8 mg m^{-2}). Mean biomass was highest at site III (20.5 mg m^{-2}), and lowest at site IV (3.0 mg m^{-2}). Production was lowest at all sites during winter (late July/August to January) and highest during spring (March to May/early June). The cohorts settling in March–May to July had the highest production values at all sites, except the first cohort of 2013 at the deepest site IV. At site IV the cohort settling in early July had

relatively high production for this site. The proportion of the total secondary production by individual cohorts differs between sites and seasons. At site I the first settling cohorts of the year cover the largest proportion of the total secondary production (49 and 36 % of total secondary production for C2 and C4, respectively). At site II the first cohorts (26 and 39 % of total secondary production for C2 and C5, respectively) and also the third cohort of year 2013 settling in October (29 % of total secondary production) are responsible for most of the secondary production. At site III by far the most productive cohort was the first cohort settling in April 2013 (95 % of total secondary production). At site IV, however, the early July cohort and the first cohort of 2014 were the most productive ones (31 and 29 % of total secondary production, respectively). The P/B -ratio was highest for the *Marenzelleria* spp. population at site III, 8.9 for the study period. The cohort-wise P/B -ratios differed at all sites with the spring and summer settlers having highest P/B -ratios at sites I, III and IV (8.9, 10.0 and 4.7, respectively), and, the autumn settlers at sites II and V (11.2 and 4.2, respectively). The P/B -ratios of the whole population for sites I–V varied between 3.3 (site V) and 8.9 (site III).

4 Discussion

We have demonstrated widely contrasting population dynamics of *Marenzelleria* spp. for our five study sites, with the deep, muddy site hosting the most stable population of *Marenzelleria* spp. though with the lowest average density over the year. The highest average density of worms over the year was observed at the 20 m deep, muddy site, followed by the sandy, shallow site at 6 m depth. All in all three species of *Marenzelleria* spp., *M. viridis*, *M. neglecta* and *M. arctia*, occurred at the study sites, with all three of them co-occurring at sites I to III, *M. arctia* being the only species observed at the deepest site IV, and *M. viridis* and *M. neglecta* inhabiting the sandy, shallow site V. Production and growth of *Marenzelleria* spp. was lowest during winter at all sites and highest during spring. Some cohorts had very high P/B -values reflecting their life history and adaptations to seasonal environments. As opportunistic species, spionids are capable of efficiently consuming the available resources, which could make them potentially more adapted to be invasive (cf Zajac 1991ab, Çinar 2013). The input of organic matter to the sea floor varies seasonally being in general highest at the study site in spring, and late summer (Heiskanen and Tallberg 1999). The spring input is visible as the increase in OM content from March to June depending on the year and site. Increased organic matter loading can increase the biomass of burrowing animals and enhance the benthic-pelagic coupling (Josefson and Conley 1997). The peaking densities following the settling from March to May at the shallowest muddy site I correspond to decreases in the sediment organic content reflecting the capability of *Marenzelleria* spp. to effectively consume the available resources. At the shallow sandy site V the sediment is poor in organic matter, but the density of *Marenzelleria* spp. nevertheless follows the changes in organic content reflecting the capacity of the population to respond to increased food availability in contrast to the muddy sites already rich in organic matter. At the deepest muddy site IV the density peaks in July and June coincide with low C/N ratio indicating the importance of fresh organic matter as a food source to the benthos.

M. viridis has been found to be more tolerant towards hypoxia, which has been thought to be one reason for their successful invasion (Schiedek 1997). At sites I and II the densities follow oxygen concentrations with low densities when oxygen concentration decreases, and higher densities due to recruitment in spring, when also oxygen concentration increases. At sites III and IV on the other hand, the increases in the density of *Marenzelleria* spp correspond to decreases in oxygen concentration. The summer thermocline at the deeper sites III and IV prevents the mixing of the water column during summer, causing a decrease in the oxygen concentration in the bottom water due to degradation and respiration processes consuming oxygen. This probably just happens to coincide with the high densities at these sites. Given that the oxygen concentration never dropped below critical levels (minimum 4.98 mg l⁻¹ at site IV in August 2013, threshold for hypoxia 2 mg L⁻¹

¹), it is unlikely that oxygen concentration would have directly impacted the densities of *Marenzelleria* spp. At the shallower sites the peaks in oxygen concentrations follow the onset of primary production and the complete circulation of water masses in spring, and the coinciding increases in densities could also be partly due to the movement of worms to these sites following the movement of the water masses as the settling of the larvae happens during this time.

The discovery of all the three species across the study sites, in addition to being important new information for this area, is probably causing the differing patterns in population dynamics between the sites. According to our analyses, the deepest site IV is inhabited only by *M. arctia*, which would suggest that this species is settling in June–August. The reproduction biology of *M. arctia* is largely unknown (Hartmann-Schröder 1996, Jirkov 2001), but juveniles have been found in April, and from the beginning of July to August in the species' native range (Sikorski and Bick 2004), matching our observations. At site III, the massive settling in June–August could thus also be attributed, at least partly, to *M. arctia*. The individuals settling from January until May could belong to *M. viridis*, which is in agreement with the recruitment in their native range in North America (Sardá et al. 1995), on a sandflat in Delaware Bay (Miller and Ullman 2004), and in the southern Baltic Sea (Simm et al. 2003, Bochert 1997). All three species could also have several periods of recruitment during the year as has been discovered e.g. for the spionid *Polydora ligni* (Zajac 1991b), but due to the uncertainty in the proportions of these species in the communities, it is not possible to appoint the recruitment bursts to certain species. This requires further targeted genetic studies. At sites II, III and V there is also one cohort settling in October, which could be *M. neglecta* although *M. viridis* has been suggested to be capable of breeding twice a year in Pärnu Bay, Estonia (Simm et al. 2003), however the species identity in the Estonian case is uncertain. This is similar to many other earlier studies on *Marenzelleria* in the Baltic Sea, where the species was identified as *M. viridis*, before it was realized that there are three species of *Marenzelleria* in the Baltic and that genetic analyses are necessary to differentiate between the species. Possibly the spring and autumn planktonic larvae found by Simm et al. (2003) could belong to different species. Bochert and Bick (1995) and Bochert (1997) also found spawning individuals of *Marenzelleria* spp. both in spring and in autumn in the southern Baltic Sea, and Bochert (1997) later confirmed autumn spawners to belong to *M. viridis* Type II, later confirmed to be *M. neglecta* (Bastrop et al. 1995, 1997, 1998, Sikorski and Bick 2004). In their native range, *Marenzelleria viridis* is found to only spawn in spring (George 1966, Atkins et al. 1987, Essink and Kleef 1993), whereas *M. neglecta* pelagic larvae have been found in the water column from September until March (Bochert 1997, Sikorski and Bick 2004).

Apart from sites IV and V, the densities of *Marenzelleria* spp. drop markedly, even to zero, during winter, an observation also similar to Sardá et al. (1995) for *M. viridis* in the species' native range. The adults of *M. viridis* show nocturnal swimming behavior (Dauer et al. 1980), also common in other polychaetes such as *Bylgides sarsi* (Sarvala 1971), which suggests the adults can move away from the sites. They could also bury deeper into the sediment, thus avoiding being caught. The cores, however, extend down to 30 cm depth at the muddy sites, 25–35 cm being the maximum depth range recorded for *M. viridis* and *M. neglecta* (Renz and Forster 2013, 2014), thus it is likely that we have sampled a representative proportion of the population. The large individuals observed again in the samples in spring likely belong to the overwintering population from the previous year producing the spring cohorts, a common finding also in other polychaetes (cf. Souza and Borzone 2000, Zajac 1991b). Also Sardá et al. (1995) recorded the largest individuals in May. This would be in concordance also with the observed larval period of 4 to 12 weeks for *M. viridis* (Bochert et al. 1997). All our study sites seem to function as spawning and settling sites, but whereas sites III, IV and V also have a population of adults present over the year, at sites I and II adults are only observed prior to spawning and only very sporadically during the rest of the year.

Comparisons between sites where *M. viridis* has been observed as a native or non-native sometimes show contrasting findings of population dynamics, densities and biomass production. Relative to the densities and biomasses of *M. viridis* observed in its native range, the densities, biomasses and production observed in the Baltic Sea seem to be lower (cf. Sardá et al. 1995). Observations of Sardá et al (1995) of the *M. viridis* population nearly disappearing during winter due to freezing conditions and/or competition for food and predation in their native range are in contrast with the observations of Miller and Ullman (2004) from Delaware Bay, where a more or less stable *M. viridis* population is found to occur in a submarine groundwater discharge area in the ocean. The species is the numerical and biomass dominant at the site in Delaware, occurring in numbers of approximately 2000 individuals per square meter but otherwise the species richness in this area is low. Our observations confirm a crash in the densities during winter at the muddy sites I to III with all three species co-occurring, but not at the sandy site V with *M. viridis* and *M. neglecta*. The densities observed at the sandy site V are also comparable to Miller and Ullman (2004). Because all worms found in the samples were not analyzed genetically we cannot distinguish relative densities and biomasses of the different species at sites I to III, where all three species co-occur, and V, where two species co-occur. Predation is a likely cause to the decrease in density, but a similar predation pressure should cause a crash in densities also at site V, where we would also expect a more intense competition for food due to the lower organic content and higher abundances of other fauna. Winter 2013-2014 was warmer than average, so freezing temperatures should not have affected the *Marenzelleria* spp. population.

In its non-native areas on the US Pacific coast, in San Francisco Bay estuary, *M. viridis* tends to occur in low-saline, low-diverse assemblages averaging only five species per sample being the characteristic species of these communities with a density similar to that found in Miller and Ullman (2004) (Ranasinghe et al. 2012). The first observations of *M. viridis* at these sites were made in 1991, when the species occurred at densities up to 1700 individual per square meter (Cohen and Carlton 1995). This happens to be around the same time the first observations of the species were made in the northern Baltic Sea (Norkko et al. 1993, Stigzelius et al. 1997). In SF Bay, *M. viridis* dominates the communities with *Corophium alienense*, and the Asian clam, *Potamocorbula amurensis*, even though the densities observed are much smaller (up to 400 ind m⁻²) than in our study area (Lee et al. 2003). The total number of species, however, is much smaller in the non-native-dominated SF Bay assemblages (approximately 5 species per sample; Thompson et al. 2013) than in our samples (over 10 for sites I to III and V) suggesting that the higher native species richness could prevent the dominance by *Marenzelleria* spp. in the Baltic Sea case. Interestingly, the Baltic Sea due to its naturally low species richness and the frequent disturbances occurring in the system, is thought to be very vulnerable to species invasions (Leppäkoski et al. 2002), but the establishment of *Marenzelleria* spp. has not meant replacements in species composition in the native benthic communities at all study sites numerically dominated by *M. balthica* at almost all sampling occasions. *Marenzelleria* spp. are numerically dominant at the peak settling period from March to May at the muddy sites I to III and V, and at site III also during summer. After excluding *M. balthica*, *Marenzelleria* spp. dominates the communities in biomass at all study sites. In its native area, *M. viridis* is never dominant in density, but during summer in biomass (Sardá et al. 1995). High densities of *M. balthica* can reduce recruitment of other infaunal species (Hines et al. 1989), and the densities of *M. balthica* in the study area increased rapidly prior to the arrival of *Marenzelleria* spp. after densities of *Monoporeia affinis* decreased drastically (Kauppi et al. 2015). The high densities of *M. balthica* could thus theoretically be able to control the densities of *Marenzelleria* spp. Further, the *M. affinis* -population, found to interfere with *M. balthica* recruitment (Elmgren et al. 1986), has shown signs of recovery (pers.obs.), likely generating interesting interactions between these three species in the future. At the shallower sites predation and/or competition by *Hediste diversicolor* is likely to contribute partly to the decrease in the numbers of *Marenzelleria* spp. between sampling occasions (pers.obs., Essink and Kleef 1988).

Also both benthivorous, piscivorous and planktivorous fish are predators of all life stages of *Marenzelleria* spp. (Winkler and Debus 1996).

At site IV, *M. arctia* is the second-most dominant species both numerically and in biomass during the whole year after *M. balthica*. In its native area in the Russian Arctic, *M. arctia* occurs in densities up to 860 ind m⁻² (Deubel et al. 2003), where it sometimes is the single species dominating the communities forming 26 % of total abundance, and 62 % of total biomass (Jørgensen et al. 1999). The abundance is lower than our observations for *M. arctia* at site IV, but the biomasses of *M. arctia* observed in the native area seem to be higher than the biomasses observed at site IV (Jørgensen et al. 1999). Also the salinities are higher at these sites ranging from 12 to 34 (Deubel et al. 2003, Jørgensen et al. 1999) although *M. arctia* is reported to be extremely freshwater tolerant and thus dominating the estuaries in the Russian Arctic (Jørgensen et al. 1999, Fetzer 2004). It has been found in widely varying conditions with salinities ranging from 0 to 31.5 and temperature from 0 to 12 °C, with salinities 3-16 suggested to be the most favourable (see Sikorski and Bick 2004 and references therein). This has likely facilitated the invasion into the Baltic Sea where seasonal changes in e.g. temperature are notable (Leppäranta and Myrberg 2009).

Highest biomass production and fastest growth measured in width of the individuals was exhibited by the spring cohorts, typical of species with opportunistic life histories (e.g. Zajac 1991ab). Also the October cohort at sites II, III and V exhibited relatively high biomass production. Secondary production and growth are enhanced by phytoplankton blooms and mixing of the water column may enhance the availability of the primary production to the benthos suggesting that the production of these cohorts would be enhanced by the spring bloom, and by the total circulation of the water column during autumn also visible as an increase in the organic matter content of the sediment in October and/or November. Fall season was found to be important in the breeding cycle of *M. viridis* suggesting the population at sites II, III and V could benefit from nutrient input due to the circulation of the water column at this time (Miller and Ullman 2004). Mean annual production found for spionids generally ranges from 0.08 to 8.06 g AFDW m⁻² per year (Souza and Borzone 2000, Ambrogi 1990) indicating that *Marenzelleria* spp. has a very high production at all of our study sites. *M. viridis* has a high capacity for secondary production for example in North American salt marshes (Sardá et al. 1995). The high productive capacity for this species could also have facilitated the establishment and success in the Baltic Sea. The production values of *Marenzelleria* spp. are, however, in general lower when compared to other polychaete orders (Abrantes et al. 1999, Kristensen 1984, Ambrogi et al. 1995). Contrastingly at site III both juveniles and adults of all three *Marenzelleria* species seem to thrive and the production is very high. Also in comparison to total secondary production of a typical deeper (46 m) northern Baltic macrobenthic community from the 1970's, the production of the *M. arctia* population alone at the similar site IV is approximately 4 g m⁻² y⁻¹ higher (10.6 g dwt m⁻² y⁻¹ in 2010's compared to 6.8 g dwt m⁻² y⁻¹ in the 1970's; Cederwall 1976). The total secondary production is thus a lot higher now than in the 1970's due to the arrival of *Marenzelleria* spp. and probably due to higher primary production (HELCOM, 2010). However, due to the changes in the dominance relationships in the communities, for example due to the increase in abundance and biomass of *M. balthica*, direct comparisons are difficult to perform.

The growth parameter K estimated from the von Bertalanffy growth equation is highest for the spring and summer cohorts. These cohorts are thus growing faster and larger, which is also reflected in their larger size compared to other cohorts. Settling in spring before the dominant species in the area *M. balthica* gives them a head start to the abundant food resources both brought down by the settling spring bloom but also available in the water column for the pelagic larvae (Burckhardt et al. 1997). The co-occurrence of three species and the uncertainty of the proportions are likely to complicate the estimations of the growth parameter K, since the species differ in their infinite size

affecting the curve estimation. When estimated for all the cohorts combined, site IV with observations of only *M. arctia*, has the largest K, whereas site V with observations of only *M. viridis* and *M. neglecta* has the lowest K, indicating that *M. arctia* would exhibit faster growth than the other two. However, when estimated for the different cohorts separately, the K at the two sites are rather similar, especially for the initial phase of growth before the plateau. Due to the sampling technique at site V (cores collected by divers from the hard, sandy sediment), we might have missed some of the larger individuals burrowing deeper into the sediment as we only managed to sample the first 8 cm of the sediment. The hard sediment, however, might prevent the polychaetes from burrowing much deeper. The spring and summer cohorts seem to be affected by either intra- or interspecific competition, or both, at all the sites. Spring and summer are characterized by the highest number of species and highest densities of all species at all sites, thus competition for food and space is likely to occur. The lowest growth rates of the individuals are observed at all sites towards the end of the summer and in winter are also indicative of the effect of a decrease in resources (primary production) and increase in competition of these resources (especially the large number of settling *M. balthica*). The cohorts settling in fall (October) also seem to have lower growth rates overall compared to the cohorts settling in spring and summer. Highest turnover rates were also observed for the spring cohorts, except for sites II and V, where the October (II) and July (V) cohorts had highest turnover rates. Overall the mean biomass and secondary production at all sites except site III is below that found in the native range. At site III, all three species together seem to contribute to the very high secondary production of *Marenzelleria* spp. and a high P/B ratio. The elimination to biomass -ratio at this site is actually negative, suggesting this site might receive individuals from the adjacent sites. Reasons behind the high mean biomass and production at site III could include, firstly, co-occurrence of all three species at this site, and secondly, contrary to sites I and II, this site has a much higher organic content in the sediment, thus possibly enabling the higher production. The production and elimination calculations could have been affected by the potential movement of adults from one site to another, which might cause the differences in the P/B and E/B -values. Spionids have in general high P/B ratios and short life spans, which is evidence of opportunistic behavior for the entire group (Sardá et al. 1995). Indeed they also rank the highest in terms of number of non-native species of all polychaetes with globally 53 species (18 % of the total number of non-native polychaetes) (Çinar et al. 2013). Compared to other polychaetes with a mean life span of one year, the turnover rates for *Marenzelleria* spp. populations at sites I and III are higher than generally observed for polychaetes (7.3 and 8.9, respectively), and for sites II, IV and V they are in the same range (3.9, 3.6 and 3.3, respectively) (e.g. Souza and Borzone 2000, Sardá and Martin 1993, Ambrogi 1990). In comparison, for the very productive and tolerant opportunist polychaete *Capitella capitata* P/B ratio of 36, and a secondary production of 270 g m⁻² y⁻¹ have been observed (Méndez et al. 1997).

In a study of *Marenzelleria* spp. densities along the southern Finnish coast, Kauppi et al. (2015) found the depth of around 30 meters to divide the *Marenzelleria* spp. population into two groups: shallower with smaller densities, and deeper with higher densities. The depth at which *M. viridis* is observed in its native, and non-native areas in North America corresponds to the depths for observations in our study sites (Ranasinghe et al. 2012, Miller and Ullman 2004, Sardá et al. 1995). Based on the results from this study, the high densities in the deeper areas would be caused by *M. arctia*. *M. arctia*, as the name indicates, is an arctic species preferring cold waters, which is probably why it reaches high densities in deeper areas below the summer thermocline. Deeper areas also have less species in total than the shallower areas (e.g. Hewitt et al. 2016, Kauppi et al. 2015), meaning possibly less competition and predation, as well as sediments with a higher organic content and thus possibly more abundant food resources. Their settling in May–August gives access to abundant resources both for the pelagic larvae due to the spring bloom of phytoplankton, and for the newly settled individuals from the settling summer bloom. *M. neglecta*, if settling in October, has a cold, dark winter with very little food ahead, but on the other hand less competition, whereas the

massive numbers of *M. viridis* recruiting in spring seem to suffer from competition at their settling sites. Karlson et al. (2015) suggested based on isotopic niche analysis that *M. arctica* would have invaded an available niche in the Baltic Sea. Similar analyses would be interesting in the case of *M. viridis* and *M. neglecta* as these do not seem to have reached as high densities as *M. arctica*. Invasibility depends both on the species' traits and on the properties of the ecosystem being invaded: the requirements of *M. viridis* and *M. neglecta* for their habitat might also have limited the increase in their densities. The environment in the native range and in the North Sea for *M. viridis* and *M. neglecta* differs considerably from the Baltic (George et al. 1966, Atkins et al. 1987, Essink and Kleef 1993). In the Baltic Sea the lack of tidal cycle, which periodically exposes the mudflats in the native ranges could have enabled the range expansion of *M. viridis* and *M. neglecta* by freeing them from the stress caused by short-term fluctuations in the environmental conditions.

In the context of species extinctions and invasions it becomes increasingly important to know the species and its biology and ecology. The functional traits of the individual species and the proportions of them in the community are important both for community structure and ecosystem functioning (Hooper et al. 2005). The role of *Marenzelleria* spp. in nutrient cycling has been studied vigorously in the Baltic Sea (e.g. Hietanen et al. 2007, Renz and Forster 2013, 2014, Kristensen et al. 2011). It has been suggested to mitigate eutrophication due to its bioturbation activities oxygenating the sediment and thus binding phosphorus (Norkko and Reed et al. 2012). There are differences in the effects between the different species (Renz and Forster 2013, 2014), and thus it is imperative to know which species we are dealing with. Population dynamics of individual species are also an essential feature determining their relative importance for cycling of material and energy in a system. Kauppi et al. 2017 found a large effect of the worms on nutrient fluxes especially in spring during the time of high food input to the benthos following the spring bloom at two site used in this study, II and IV. From the point of view of nutrient cycling and combining the information with their population biology, it seems the worms are efficient in processing the settling organic material, thus their effect on nutrient cycling is dependent on the amount and timing of organic matter input, and the success of their reproduction producing the settling worms.

5 Conclusions

Since their introduction to the Baltic Sea, the polychaete genus *Marenzelleria* spp. has become one of the most dominant members of the benthic communities in the Baltic Sea. Depending on the habitat they are occupying, the populations in the northern Baltic Sea show differing seasonal dynamics in density and biomass, with differing species identities of *Marenzelleria* spp. in these habitats, and partly the biotic and abiotic conditions. *Marenzelleria arctica* seems to be occupying predominantly muddy areas in all depths, whereas, *M. viridis* and *M. neglecta* seem to prefer shallower (above 20 m) depths, and sandier areas. The juveniles occur in high numbers during early spring-early summer and late fall at the shallower areas (above 20 m), and in spring and late summer in deeper areas (over 20 m). At around 20 m depth, where all three species co-occur and reproduce, the mean density, biomass and production of the genus is highest. Compared to the native areas, the densities observed are higher, but biomasses lower. The seasonal dynamics at the shallow (5-10 m) muddy sites are comparable to native areas with a crash in densities during winter possibly due to predation and/or competition, or movement of adults either away from these sites or to deeper layers of the sediment. Organic matter input is likely to affect the population densities and biomasses at the more organic-poor, shallow sites with implications of both intra- and interspecific competition, whereas oxygen concentrations, temperature and salinity in the bottom water correlate with the densities at the deeper sites, likely also indicating the effect of both the horizontal and vertical movement of the water masses on organic matter input, and possibly movement of the worms. Despite their apparent success in establishment, the dominant species in numbers and in biomass during most of the year and in most areas, is the native Baltic clam, *M. balthica*. The

seasonally large numbers of *Marenzelleria* spp. are likely to compete with native fauna for resources, provide an abundant food source for predators, and are important for organic matter processing in the system, all of which remain interesting questions especially in the face of climate change, which will likely change the seasonal patterns of energy flow into and out of the system. More studies on the distribution of the three species and their effects on the species interactions in the surrounding community and on ecosystem functioning in the habitats they occur in are still needed in order to fully understand the importance of the species complex in the system.

Acknowledgements. This study was supported by Nordenskiöld samfundet r.f., Jenny and Antti Wihuri Foundation, Walter and Andrée de Nottbeck foundation (grants to LK), the BONUS COCOA-project supported by BONUS (Art 185), funded jointly by the EU and the Academy of Finland, and the University of Helsinki (3-year grant to JN). We would like to thank Prof Roman Zajac for helpful comments on the manuscript. We also wish to thank Dr. Ralf Bastrop at the University of Rostock for performing the genetic analyses, and Samu Elovaara, Henri Jokinen, Julia Scheinin, Camilla Gustafsson, Anna Jansson, Johanna Gammal, the trainees and personnel at Tvärminne Zoological Station for the invaluable help in the field and in the lab.

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Figure 1. Densities (mean+SD) and biomasses (mean+SD) of *Marenzelleria* spp. at the study sites I-V along a depth gradient from April 2013 to June 2014. Embedded a map showing the geographical distribution of the study sites. Map from the National Land Survey of Finland.

Figure 2. Seasonal variation in the densities of *Marenzelleria* spp. (on the left y-axis), and the significantly correlated environmental factors (on the right y-axis) from April 2013 to June 2014 at sites I-V. DO=dissolved oxygen in the bottom water in mg L⁻¹, OM=organic content of the sediment measured as LOI (%).

Figure 3. Size frequency distributions of *Marenzelleria* spp. at the sites I-V from April 2013 to June 2014, a=I, b=II, c=III, d=IV and e=V. C1 to C5 refer to the cohorts present. Note the different scale on the axes.

Table 1. Environmental parameters measured at the sampling sites from April 2013 to June 2014. DO=dissolved oxygen in mg L⁻¹, LOI=Loss On Ignition=organic content of the sediment in %. All hydrography measures from near-bottom water (<1 m).

Table 2. Pearson product moment correlations between densities at time t and time t+1 and environmental factors at the study sites I-V. DO=dissolved oxygen in the bottom water in mg L⁻¹, OM=organic matter content in the sediment measured as LOI (%). Significant correlations are highlighted.

Table 3. Results from the general von Bertalanffy growth equation for the whole population at sites I-V, and for the separate cohorts at sites IV and V. init refers to the initial phase of growth before the plateau is reached.

Table 4. Individual growth rates (in mg dwt) for the different cohorts at sites I-V from April 2013 to June 2014.

Table 5. Correlations between mean individual growth rates for cohorts and densities of *Marenzelleria* spp. in the cohorts, density of other taxa, number of taxa and the total density of *Marenzelleria* spp. “M. C2” refers to *Marenzelleria* spp. density in cohort 2 and so on, “Other taxa” is the density of other taxa combined, “*Marenzelleria* spp.” is the total density of *Marenzelleria* spp.

Table 6. Production calculations for sites I-V. P=biomass production, E=biomass elimination, mean BM=mean biomass, P/B=production to biomass -ratio, E/B=elimination to biomass -ratio. Subscript tot refers to the sum of the cohorts.

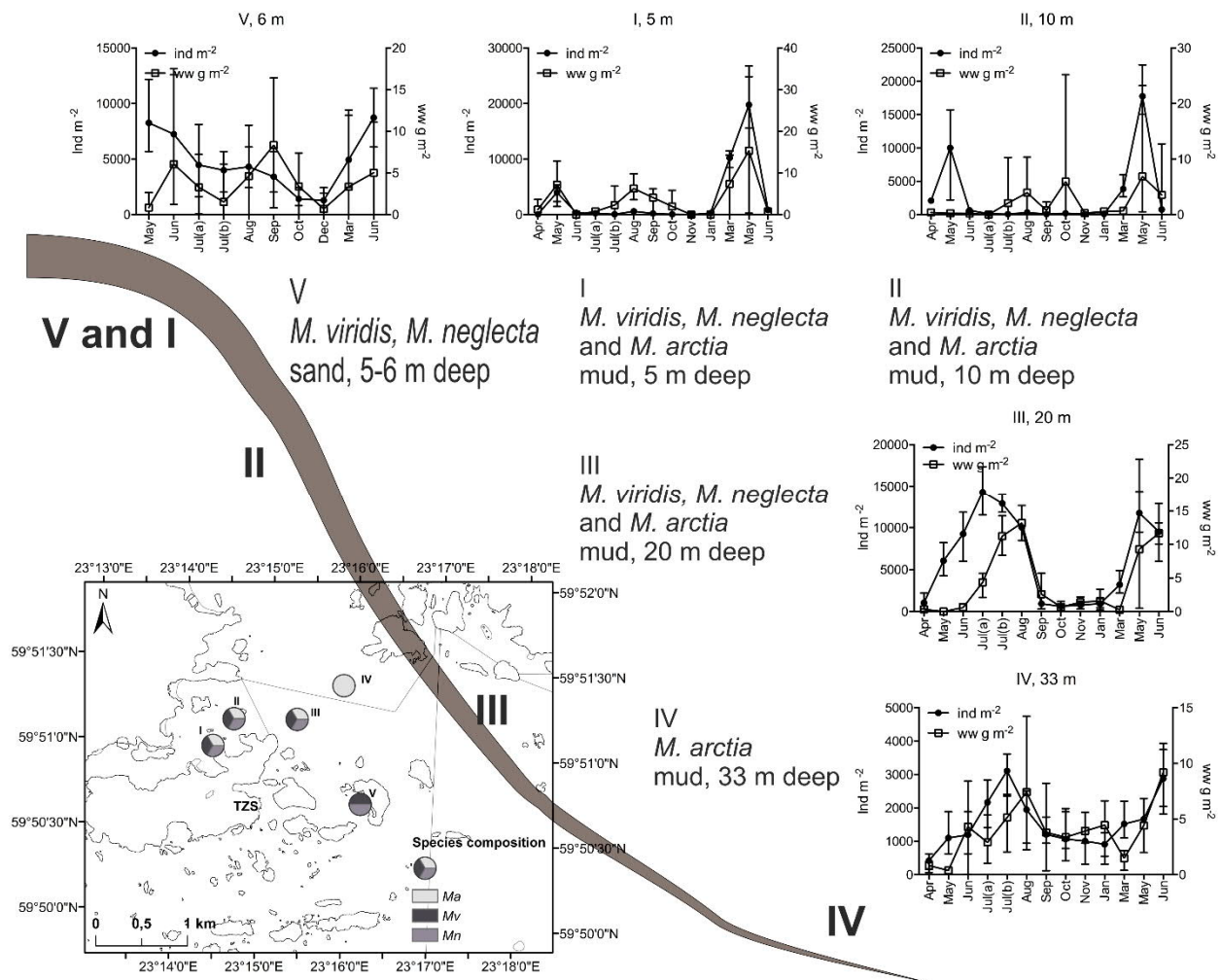


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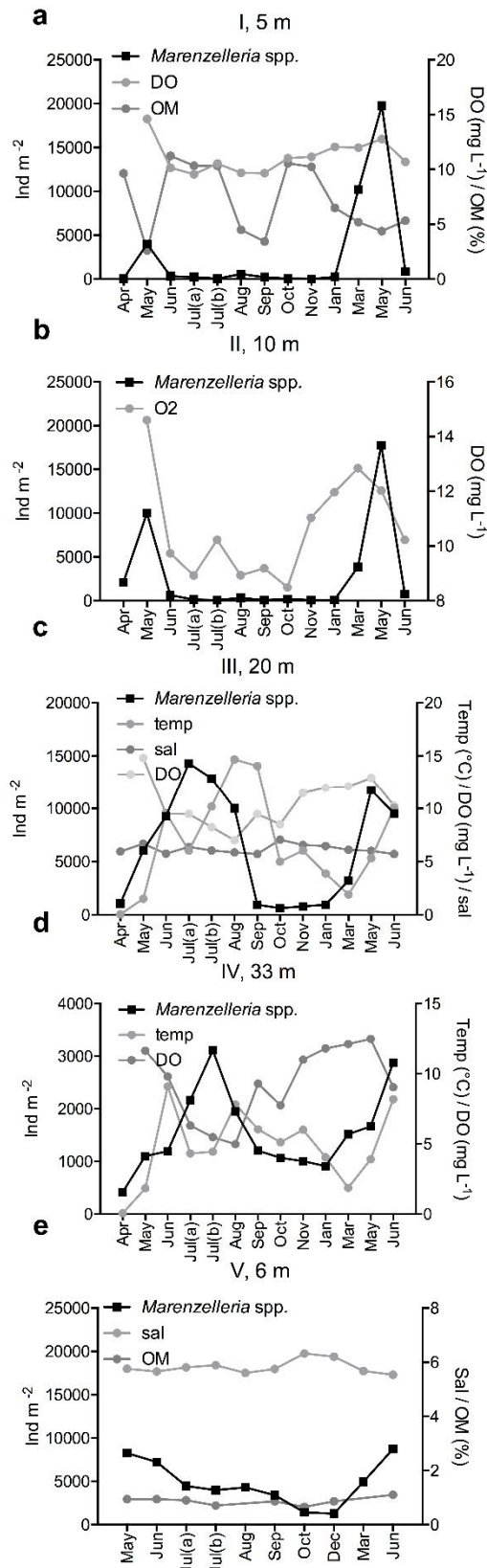
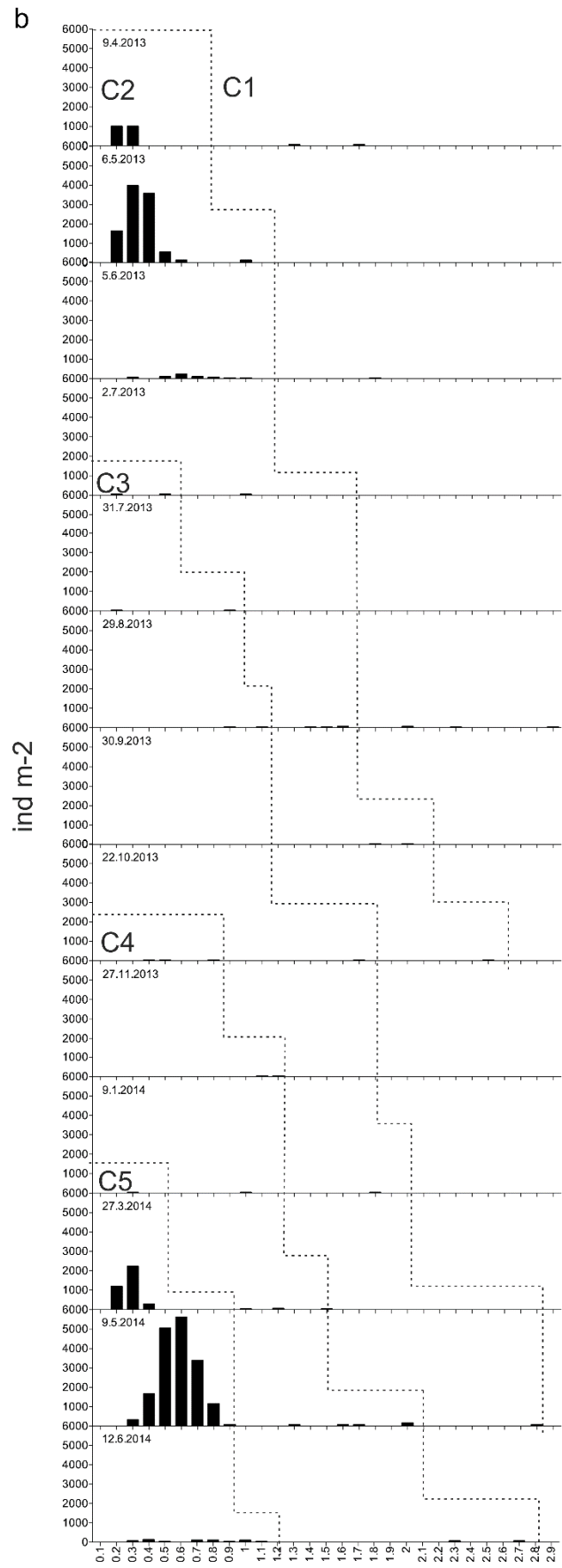
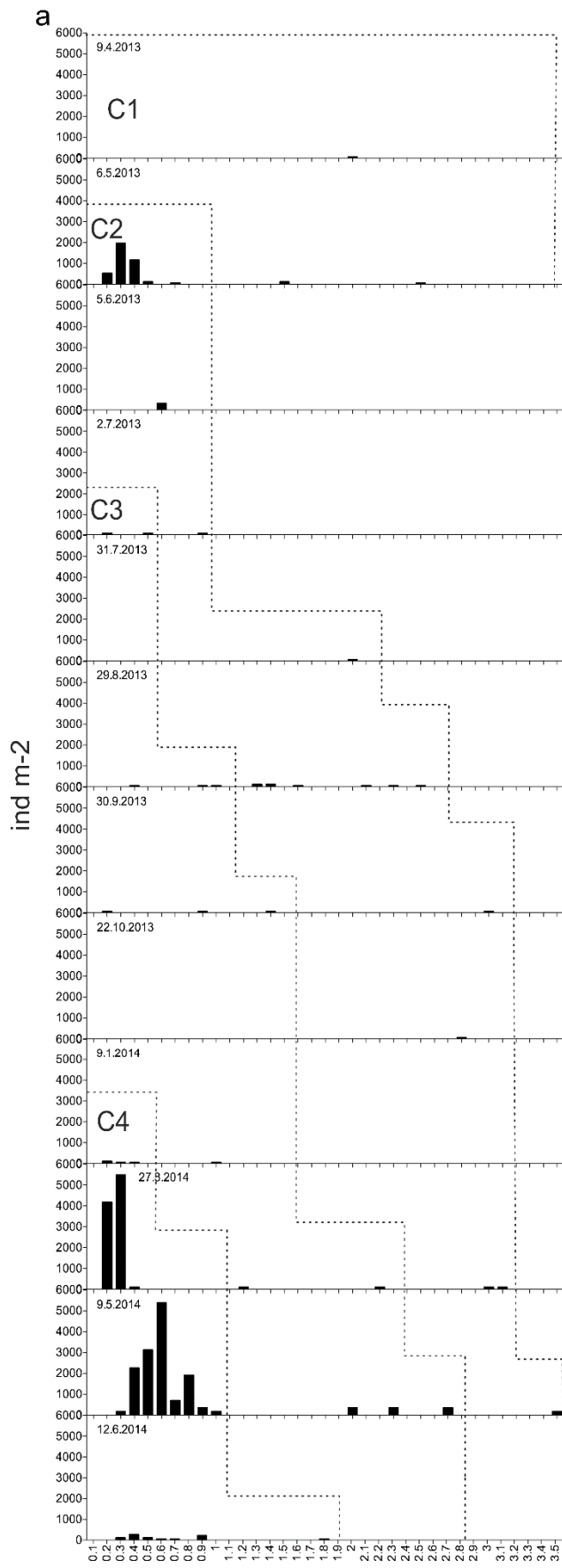
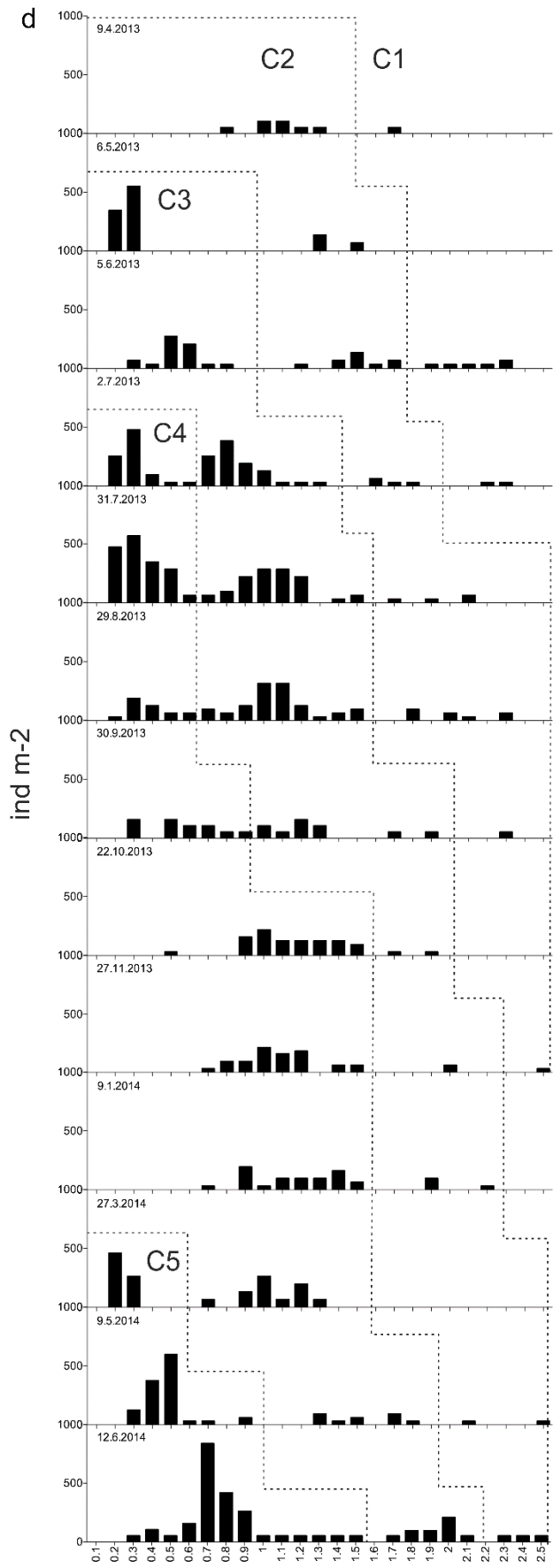
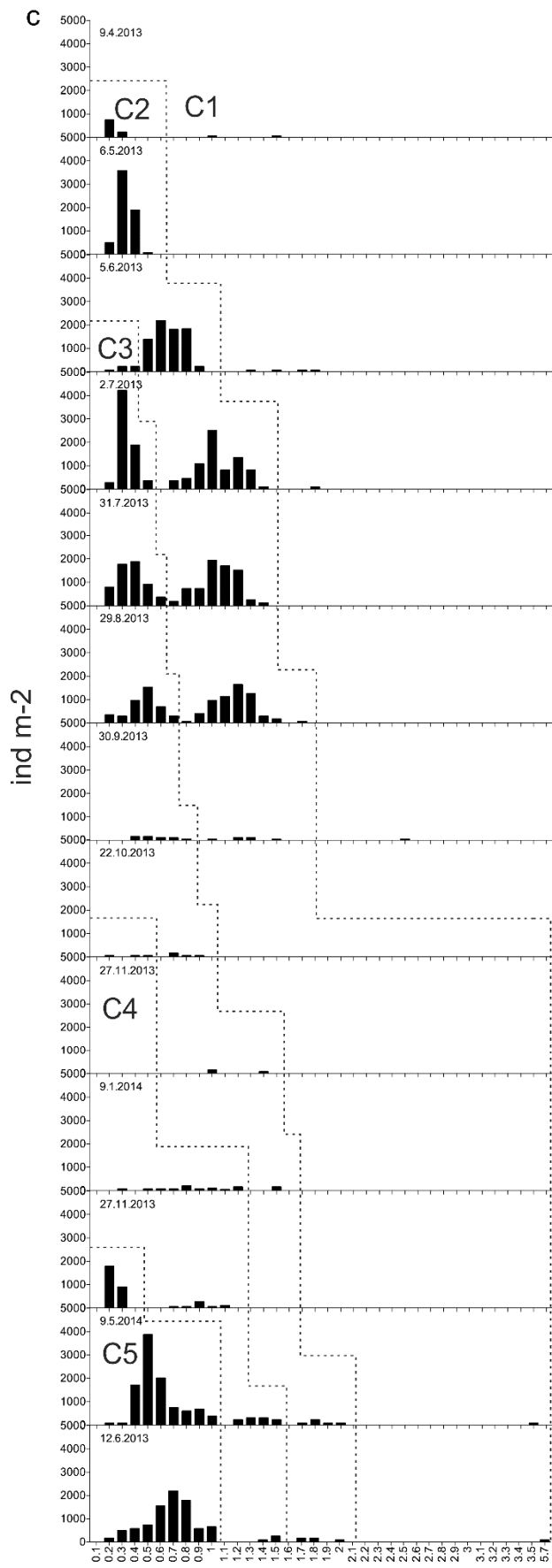


Figure 2. Seasonal variation in the densities of *Marenzelleria* spp. (on the left y-axis), and the significantly correlated environmental factors (on the right y-axis) from April 2013 to June 2014 at sites I-V. DO=dissolved oxygen in the bottom water in mg L^{-1} , OM=organic content of the sediment measured as LOI (%).





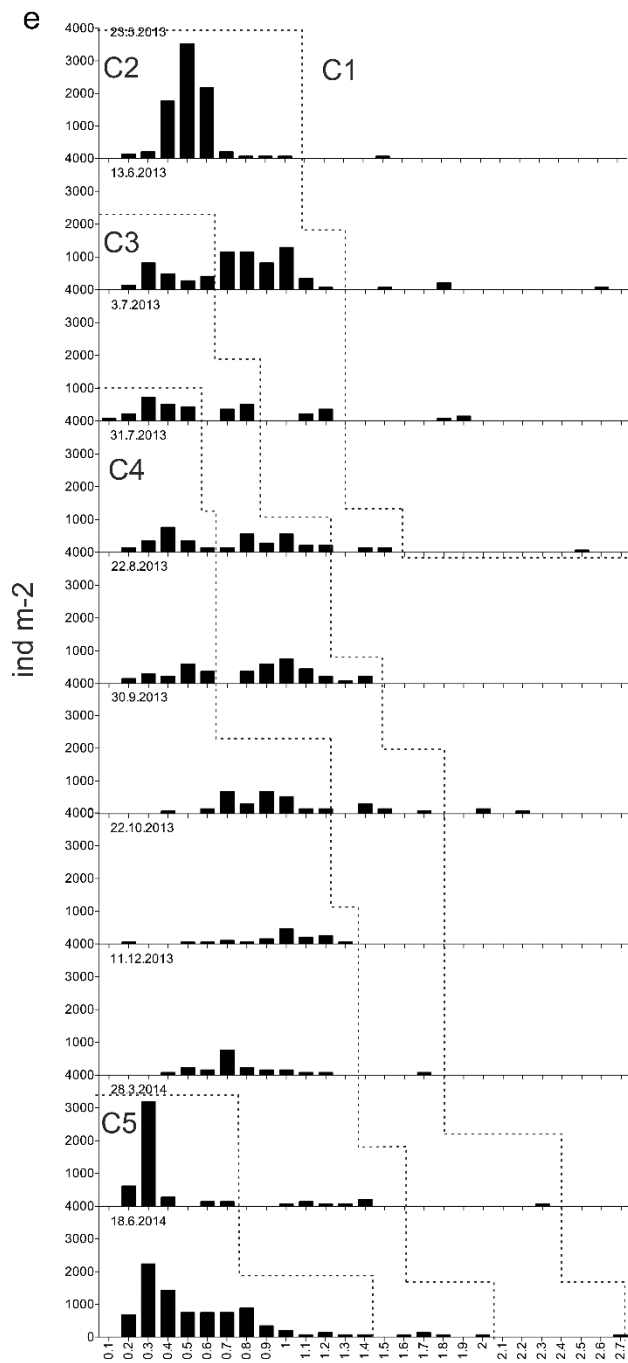


Figure 3. Size frequency distributions of *Marenzelleria* spp. at the sites I-V from April 2013 to June 2014, a=I, b=II, c=III, d=IV and e=V. C1 to C5 refer to the cohorts present. Note the different scale on the axes.

Table 1. Environmental parameters measured at the sampling sites from April 2013 to June 2014. DO=dissolved oxygen in mg L⁻¹, LOI=Loss On Ignition=organic content of the sediment in %. All hydrography measures from near-bottom water (<1 m).

Site Month	I (5 m, mud)					II (10 m, mud)					III (20 m, mud)					IV (33 m, mud)					V (6 m, sand)				
	Temp	Sal	DO	OM	C/N	Temp	Sal	DO	OM	C/N	Temp	Sal	DO	OM	C/N	Temp	Sal	DO	OM	C/N	Temp	Sal	DO	OM	C/N
Apr	0.6	5.7		9.6	7.3	0.1	6.0		5.3	7.3	0.0	5.9				0.1	6.0								
May	3.9	5.9	14.6	2.6	7.3	2.4	6.3	14.6	5.5	7.3	1.5	6.7	14.8	13.5	7.4	1.8	7.0	11.7	14.8	6.7	9.8	5.8		0.9	7.0
Jun	12.8	5.7	10.2	11.2	7.6	11.2	5.7	9.7	7.5	6.9	9.6	5.7	9.5	12.5	7.5	9.1	5.8	9.8	14.4	6.7	10.0	5.7	10.3	0.9	
Jul(a)	11.3	4.6	9.6	10.3	7.1	8.9	6.0	8.9	7.9	7.0	6.0	6.4	9.5	11.6	7.0	4.3	6.7	6.3	13.6	7.1	12.0	5.8	9.4	0.9	7.4
Jul(b)	16.1	5.9	10.5	10.3		14.9	5.9	10.2	7.6	6.8	10.2	6.0	8.2	11.2	7.3	4.4	6.7	5.5	13.6	6.7	16.1	5.9	10.6	0.7	7.1
Aug	16.0	5.6	9.7	4.5	7.2	15.5	5.8	8.9	10.0	7.0	14.7	5.9	7.0	11.7	7.0	7.8	6.2	5.0	13.2	7.0	16.0	5.6	10.3		6.3
Sep	13.4	5.7	9.7	3.4	7.8	14.5	5.7	9.2	9.6	7.1	14.1	5.7	9.5	12.4	6.1	6.0	7.1	9.3	13.8	6.8	14.3	5.8	9.2	0.9	7.1
Oct	7.1	6.2	11.0	10.6	7.3	6.6	6.6	8.5	8.6	7.0	5.0	7.1	8.5	4.1	7.0	5.1	7.1	7.8	14.2	6.6	7.1	6.3	11.0	0.7	7.2
Nov	5.6	6.5	11.2	10.2	7.0	6.1	6.6	11.0	6.1	7.2	6.0	6.6	11.5	10.9	8.4	6.0	6.6	11.0	12.8	6.7					
Dec																					4.2	6.2	11.9	0.9	6.9
Jan	3.8	6.3	12.1	6.5	7.2	3.7	6.3	12.0	5.5	7.6	3.9	6.5	12.0	8.9	6.8	4.0	6.5	11.8	13.2	6.6					
Mar	2.3	6.0	12.0	5.2	7.2	2.1	6.0	12.8	12.5	7.8	1.9	6.1	12.1	7.0	7.2	1.9	6.3	12.1	14.1	6.9	2.2	5.7	13.6		9.8
May	5.5	6.0	12.8	4.4	6.8	5.5	6.0	12.0	11.0	7.1	5.3	6.0	12.9	11.2	6.4	3.9	6.1	12.5	15.0	7.1					
Jun	10.8	5.5	10.7	5.3	7.1	10.2	5.6	10.2	11.2	7.0	10.1	5.7	10.3	7.4	7.5	8.2	5.8	9.0	15.3	6.6	10.6	5.5	12.2	1.1	7.5

0.6	4.6	9.6	2.6	6.8	0.1	5.6	8.5	5.3	6.8	0.0	5.7	7.0	4.1	6.1	0.1	5.8	5.0	$\frac{12.}{8}$	6.6	2.2	5.5	9.2	0.7	6.3
16.1	6.5	$\frac{14.}{6}$	$\frac{11.}{2}$	7.8	15.5	6.6	$\frac{14.}{6}$	$\frac{12.}{5}$	7.8	14.7	7.1	$\frac{14.}{8}$	$\frac{13.}{5}$	8.4	9.1	7.1	$\frac{12.}{5}$	$\frac{15.}{3}$	7.1	16.1	6.3	$\frac{13.}{6}$	1.1	9.8

Table 2. Pearson product moment correlations between densities at time t and time t+1 and environmental factors at the study sites I-V. DO=dissolved oxygen in the bottom water in mg L⁻¹, OM=organic matter content in the sediment measured as LOI (%). Significant correlations are highlighted.

Site			Temp	Sal	DO	C/N	OM
I. 5 m	Density (t)	r	-0.32	0.12	0.62	-0.45	-0.68
		Sig.	0.31	0.70	0.04	0.17	0.01
		N	12	12	11	11	12
	Density (t+1)	r	-0.55	0.28	0.32	-0.18	-0.26
		Sig.	0.08	0.41	0.37	0.61	0.44
		N	11	11	10	10	11
II. 10 m	Density (t)	r	-0.57	-0.12	0.67	0.33	0.24
		Sig.	0.06	0.70	0.02	0.30	0.45
		N	12	12	11	12	12
	Density (t+1)	r	-0.64	-0.03	0.44	0.60	-0.57
		Sig.	0.05	0.93	0.24	0.07	0.08
		N	11	11	11	11	11
III. 20 m	Density (t)	r	0.24	-0.23	-0.15	0.00	0.35
		Sig.	0.41	0.44	0.64	0.1	0.24
		N	14	14	13	13	13
	Density (t+1)	r	-0.55	0.28	0.32	-0.18	-0.26
		Sig.	0.08	0.41	0.37	0.61	0.44
		N	11	11	10	11	10
IV. 33 m	Density (t)	r	0.42	-0.09	-0.59	0.18	0.21
		Sig.	0.15	0.78	0.05	0.58	0.51
		N	13	13	12	12	12
	Density (t+1)	R ²	0.12	-0.16	-0.31	0.59	0.06
		Sig.	0.74	0.64	0.39	0.07	0.87
		N	11	11	10	10	10
V. 6 m	Density (t)	r	0.15	-0.78	0.13	0.15	0.78
		Sig.	0.68	0.01	0.74	0.71	0.02
		N	10	10	9	9	8
	Density (t+1)	r	-0.17	-0.26	0.34	-0.11	0.57
		Sig.	0.68	0.53	0.45	0.82	0.18
		N	9	9	8	9	7

Table 3. Results from the general von Bertalanffy growth equation for the whole population at sites I-V, and for the separate cohorts at sites IV and V. init refers to the initial phase of growth before the plateau is reached.

Site	Cohort	SS _{res}	R ²	S _∞	K	D	t ₀	n
I		5.00	0.76	5.70	0.002	11.67	-27.55	23
II		1.42	0.89	5.70	0.002	1.07	-36.72	23
III		1.71	0.90	5.70	0.003	5.54	-25.20	30
IV		2.29	0.85	2.62	0.006	1.71	-58.78	33
V		5.71	0.59	5.30	0.001	0.99	125.11	32
<hr/>								
IV	C2	0.47	0.90	2.80	0.007	4.26	124.71	11
	C3	0.31	0.81	2.80	0.002	1.15	124.90	10
	C2 init	0.20	0.96	2.10	0.021	29.56	125.08	11
	C3 init	0.06	0.86	1.20	0.012	4.60	136.47	8
V	C2	0.01	0.99	1.80	0.019	14.47	124.28	7
	C3	0.09	0.95	2.00	0.013	6.94	124.55	8
	C4 init	0.01	0.98	1.30	0.010	4.23	127.00	8
	C5 init	0.02	0.94	1.50	0.004	1.97	125.08	4

Table 4. Individual growth rates (in mg dwt) for the different cohorts at sites I-V from April 2013 to June 2014.

Month	I. C2	I. C3	I. C4	II. C2	II. C3	II. C4	II. C5	III. C2	III. C3	III. C4	III. C5	IV. C2	IV. C3	IV. C4	V. C2	V. C3	V. C4	V. C5
Apr				0.020 0				0.005 4										
May	0.003 6			0.002 0				0.020 7				0.016 6			0.034 6			
Jun	0.017 3			0.017 8				0.019 1	0.000 0			0.026 4			0.019 1	0.026 2		
Jul(a)	0.059 0	0.011 1		0.018 0	0.012 4			0.002 2	0.006 1			0.028 4	0.019 3		0.020 8	0.013 2	0.006 0	
Jul(b)	0.000 3				0.022 3			0.009 8	0.000 0			0.012 9	0.010 5		0.017 2	0.015 4	0.012 6	
Aug	0.018 1	- 0.008 9		0.011 3	0.083 9			- 0.002 0	0.007 0			0.000 3	- 0.004 7			0.015 6	0.010 4	
Sep	0.029 9	0.006 3		0.042 1				0.015 7	0.013 4			0.000 0	0.014 1		0.001 7	0.002 9	0.006 2	
Oct	0.002 5				0.002 0	0.023 2			0.017 7	0.000 5		0.008 4	0.003 2				0.000 7	0.009 3
Nov						- 0.005 5			0.010 3	0.000 0		0.002 2	0.000 0					
Dec																0.001 0	0.003 5	0.002 1
Jan		0.015 7	0.000 0		- 0.015 8	0.005 5	0.000 1		0.004 7	0.001 1		0.003 3	- 0.002 4					
Mar	0.016 2	0.022 2	0.013 9			0.015 1	0.011 8			0.001 2	0.014 4		0.019 6	0.013 7	0.007 6		0.000 8	0.005 7
May			0.023 7			0.037 8	0.005 5	0.100 7	0.006 4	0.002 5	0.000 0	0.004 1	0.015 7	0.017 1				

Jun

0.003
7

Table 5. Correlations between mean individual growth rates for cohorts and densities of *Marenzelleria* spp. in the cohorts, density of other taxa, number of taxa and the total density of *Marenzelleria* spp. “*M. C2*” refers to *Marenzelleria* spp. density in cohort 2 and so on, “Other taxa” is the density of other taxa combined, “*Marenzelleria* spp.” is the total density of *Marenzelleria* spp.

Site			<i>M. C2</i>	<i>M. C3</i>	<i>M. C4</i>	<i>M. C5</i>	Other taxa	No of taxa	<i>Marenzelleria</i> spp.
I. 5 m	C2 (mg d ⁻¹)	r	-0.31	0.58	-0.05		0.33	-0.40	-0.15
		Sig.	0.45	0.13	0.92		0.43	0.32	0.73
	C3 (mg d ⁻¹)	r	-0.60	0.10	0.63		-0.52	0.36	0.59
		Sig.	0.40	0.87	0.26		0.37	0.55	0.29
	C4 (mg d ⁻¹)	r		0.89	0.99		-0.81	0.10	1.00
		Sig.		0.30	0.07		0.40	0.94	0.06
II. 10 m	C2 (mg d ⁻¹)	r	-0.63	-0.20			-0.18	0.18	-0.63
		Sig.	0.18	0.71			0.73	0.73	0.18
	C3 (mg d ⁻¹)	r	-0.36	0.00	0.00	-0.09	-0.24	-0.03	-0.09
		Sig.	0.53	1.00	1.00	0.80	0.51	0.93	0.80
	C4 (mg d ⁻¹)	r		-0.23	0.17	-0.01	-0.41	0.12	-0.01
		Sig.		0.66	0.75	0.98	0.42	0.83	0.98
	C5 (mg d ⁻¹)	r		0.12	0.47	0.25	-0.41	0.31	0.26
		Sig.		0.88	0.53	0.75	0.59	0.69	0.74
III. 20 m	C2 (mg d ⁻¹)	r	-0.54	-0.42	0.97	0.97	-0.39	0.04	0.19
		Sig.	0.17	0.30	0.00	0.00	0.34	0.93	0.66
	C3 (mg d ⁻¹)	r	-0.47	-0.33	-0.19	-0.27	0.10	-0.60	-0.66
		Sig.	0.17	0.35	0.60	0.45	0.78	0.07	0.04
	C4 (mg d ⁻¹)	r	0.23	-0.15	-0.17	0.44	-0.62	-0.97	0.40
		Sig.	0.77	0.85	0.83	0.56	0.388	0.03	0.60
IV. 33 m	C2 (mg d ⁻¹)	r	0.87	-0.24	-0.21		-0.36	-0.23	0.23
		Sig.	0.001	0.51	0.57		0.31	0.52	0.52
	C3 (mg d ⁻¹)	r	0.38	-0.07	0.51		0.06	-0.01	0.32
		Sig.	0.32	0.86	0.16		0.87	0.98	0.40
V. 6 m	C2 (mg d ⁻¹)	r	0.81	0.02	-0.58	-0.40	0.13	-0.43	0.77
		Sig.	0.05	0.97	0.23	0.44	0.81	0.40	0.07
	C3 (mg d ⁻¹)	r	0.75	0.89	-0.46	-0.60	0.13	-0.21	0.93
		Sig.	0.09	0.02	0.36	0.21	0.81	0.69	0.01
	C4 (mg d ⁻¹)	r	0.31	0.94	0.65	-0.53	0.19	-0.68	0.39
		Sig.	0.50	0.002	0.12	0.23	0.68	0.09	0.39
	C5 (mg d ⁻¹)	r	-0.01	-0.86	-0.06	-1.00	0.42	0.50	0.03
		Sig.	1.00	0.34	0.96	0.03	0.73	0.67	0.98

Table 6. Production calculations for sites I-V. P=biomass production, E=biomass elimination, mean BM=mean biomass, P/B=production to biomass -ratio, E/B=elimination to biomass -ratio. Subscript tot refers to the sum of the cohorts.

Site I	Cohort	P	E	mean BM	P/B	E/B
	C1	0.10	-0.86	0.13	0.74	-6.75
	C2	17.46	5.41	2.21	7.91	2.45
	C3	5.30	-7.56	1.11	4.78	-6.82
	C4	12.84	11.19	1.45	8.88	7.74
	Pop	35.70	8.19	4.89	7.30	1.67
Site II	Cohort	P	E	mean BM	P/B	E/B
	C1	0.78	-0.78	0.18	4.25	-4.25
	C2	3.32	3.30	0.83	4.01	3.99
	C3	1.00	-0.93	0.86	1.17	-1.08
	C4	3.68	1.62	0.33	11.17	4.92
	C5	4.83	4.23	1.25	3.87	3.39
	Pop	12.83	8.22	3.27	3.93	2.52
Site III	Cohort	P	E	mean BM	P/B	E/B
	C1	0.39	0.62	0.10	3.87	6.13
	C2	174.16	1.63	17.40	10.01	0.09
	C3	2.98	0.79	1.30	2.29	0.60
	C4	1.81	0.88	0.40	4.57	2.22
	C5	3.04	-4.13	1.29	2.36	-3.21
	Pop	182.38	-0.21	20.49	8.90	-0.01
Site IV	Cohort	P	E	mean BM	P/B	E/B
	C1	0.97	0.56	0.19	5.03	2.88
	C2	1.65	1.77	0.49	3.37	3.62
	C3	3.37	1.38	1.00	3.38	1.38
	C4	3.17	0.17	1.00	3.18	0.17
	C5	1.59	-1.56	0.34	4.65	-4.55
	Pop	10.75	2.31	3.02	3.56	0.77
Site V	Cohort	P	E	mean BM	P/B	E/B
	C1	1.94	1.14	0.81	2.41	1.42
	C2	4.73	11.50	1.69	2.79	6.80
	C3	5.63	4.27	1.35	4.17	3.17
	C4	4.19	2.48	1.25	3.36	1.99
	C5	2.59	-4.01	0.93	2.78	-4.31
	Pop	17.13	14.23	5.22	3.28	2.73